Host Range and Offspring Quantities in Natural Populations of *Nasonia vitripennis* (Walker, 1836) (Hymenoptera: Chalcidoidea: Pteromalidae)

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Abstract.—The gregarious ectoparasitic wasp *Nasonia vitripennis* is a well-established model organism in various aspects of genetics. In the field it is the dominant species in the parasitoid community found in birds' nests. In these nests *N. vitripennis* parasitizes the puparia of cyclorrhaphous flies. The most frequently recorded natural field host species are two ornithoparasitic bird blow flies *Protocalliphora azurea* and *P. falcozi*, the necrophagous *Calliphora vicina* (all: Calliphoridae) and the sapro-necrophagous *Potamia littoralis* (Muscidae). These field host records along with additional laboratory rearings allowed us to define the host range of *N. vitripennis*: It is restricted to Cyclorrhapha with further restrictions in size, shape and surface structure of the host species. The host acceptance excludes Hippoboscidae, Fanniidae and small species like heleomyzids and drosophilids, but includes parasitism of tachinids and sarcophagids or facultative hyperparasitism of Alysiinae (Hymenoptera: Braconidae) in calliphorid primary host puparia. The mean number of parasitoids emerging from field-collected specimens of the four regular host species ranged from 9.3 to 25.7 and the sex ratio was female-biased with proportions of males ranging from 0.13 to 0.34. This study shows that there are significant differences between host species in the number of individuals that emerged and the proportion of males. A correlation between the number of individuals and host size was indicated, but not between host size and sex ratio.

Nasonia vitripennis (Walker, 1836) (Hymenoptera: Pteromalidae) is a gregarious cosmopolitan idiobiontic parasitoid species and one of the most prominent model organisms in speciation and developmental genetics (e.g. Gadau et al. 1999; Perfectti and Werren 2001; Werren et al. 2004), but little is known about its natural life history. The most comprehensive work on this species is still the review by Whiting (1967), focused on behaviour and laboratory tests. In Europe *Nasonia vitripennis* is the only species of the genus *Nasonia*, in Northern America two additional species are present: *Nasonia giraulti* Darling, 1990 and *Nasonia longicornis* Darling, 1990 (Darling and Werren 1990).

Nasonia vitripennis has been frequently recorded from birds' nests (e.g. Abraham 1985; Darling and Werren 1990; Molbo and Parker 1996; Peters and Abraham 2004) and repeatedly recorded from carrion (e.g. Blanchot 1995; Grassberger and Frank 2004; Marchiori 2005). Carrion, as a habitat, overlaps with birds' nests as dead birds can be regularly found in nests. Within both habitats, *N. vitripennis* parasitizes numerous species of cyclorrhaphous flies such as Calliphoridae and Sarcophagidae. Records from dung show that *N. vitripennis* is not a dominant species in this habitat (Floate et al. 1999; Skovgard and Jespersen 2000; Kaufman et al. 2001; Birkemoe et al. 2008) and cannot be considered an economically important antagonist of synanthropic flies (Legner 1967; McKay and Galloway 1999).

Abraham (1985) and Abraham and Peters (2008) hypothesized that birds' nests are the primary habitat of *N. vitripennis*.

Peters (2007) corroborated that the habitat specialist *N. vitripennis* is the key species in the birds' nest parasitoid web. First field studies on *N. vitripennis* in birds' nests (Abraham 1985; Schlein 2002) were mostly made with sentinel replacement host puparia, which helped to reconstruct the parasitoids' phenology but gave little evidence regarding the natural hosts appearing in the nests. Subsequent studies (Peters and Abraham 2004; Abraham et al. 2005) reported field host records and defined a preliminary host range of *N. vitripennis* but left differences in life history patterns concerning number of offspring and sex ratio in relation to host species unclarified.

Theoretical considerations predict a correlation between host size and the number of offspring produced (Waage 1986; Godfray 1994). The correlation between host size and number of parasitoids has already been described for *N. vitripennis* under laboratory conditions by Wylie (1967) and Rivers and Denlinger (1995). In parasitoids it is generally advantageous if the sex ratio is shifted in favour of the females (Godfray 1994). However, parasitoid sex ratio is influenced by various variables and has been subject of numerous studies in the past and present. Host-quality (or host-size) model predicts that in smaller, less suitable hosts, more males are produced as the males' fitness is less dependent on host quality (Charnov et al. 1981; Waage 1986; Ueno 1999). Werren (1983), Molbo and Parker (1996) and Grillenberger et al. (2008) observed that other factors such as the parasitoid population size and the number of ovipositing females exert a strong influence on sex ratio which might suppress the predicted correlation between sex ratio and host size. These results are connected to local mate competition (LMC) theory (Hamilton 1967). LMC describes that male-male competition for mates is restricted to the natal patch. *N. vitripennis* exhibits typical characteristics predicted for a species with LMC: Sex ratio is highly female-biased if females oviposit alone,

more males are produced by superparasitizing females to maximize the opportunities of their offspring to be able to mate (Werren 1980). To a lower extent asymmetric larval competition between sexes (Sykes et al. 2007) and characteristics of mating males (Shuker et al. 2006) have been demonstrated in laboratory studies to influence sex ratio in *N. vitripennis*. Sex ratio in relation to field host species of different size might give further insight into sex ratio mechanisms in *N. vitripennis*.

In contrast to previous studies, this study presents field data on offspring quantities of *N. vitripennis* reared from different natural host species collected as puparia from birds' nests. Data are examined for any differences between host species in number of individuals per host and proportion of males and for any correlations between the size of host puparia and the number of parasitoids reared and between host size and sex ratio. Furthermore, this study utilized field collection of host puparia and additional laboratory rearings to define the host range of *N. vitripennis*. These results can circumscribe host acceptance and rejection cues of *N. vitripennis* such as shape and size of the host which are known to be used by parasitoids (Wylie 1967; Cooperband and Vinson 2000).

MATERIAL AND METHODS

Nests of *Parus* spp. (tits) were examined for the presence of puparia of cyclorrhaphous flies parasitized by *Nasonia vitripennis*. The nine collection sites were located in Germany and included: Hamburg (5 sites), (1) Hamburg-Eissendorf, "Staatsforst Haake" forest N53.4548 E09.9207, (2) Hamburg-Eissendorf, garden N53.4540 E09.9391, (3) Hamburg-Rotherbaum, "Sternschanzenpark" N53.5655 E09.9709, (4) Hamburg-Bramfeld, "Umweltzentrum Karlshöhe" park N53.6295 E10.1092, (5) Hamburg-Poppenbüttel (garden in the district of Poppenbüttel without exact locality); Schleswig-Holstein (3 sites), (6) "Linauer

Forst" forest N53.6734 E10.4897, (7) Elms-horn, garden N53.7656 E09.6725, (8) Hasel-dorf, garden N53.6352 E09.5986; Baden-Württemberg (1 site), (9) Bad Mergentheim, "Stadtwald" forest N49.5083 E09.7722 (reference system WGS84).

Puparia were stored in Petri dishes at room temperature until the emergence of parasitoids. These were preserved in 70% EtOH in pools of multiple puparia or in single puparium tubes. The latter will be referred to as "separately stored puparia" within this paper. The corresponding host puparia were taped to the EtOH tubes. The parasitoids that emerged were counted and sex was determined. Maximum length and maximum width of host puparia were measured. For puparia species identification voucher specimens of puparia and corresponding identified imagines were used that were collected during our studies on birds' nest fly fauna (Peters and Abraham 2004; Peters 2007). Voucher specimens are deposited at Zoologisches Museum Hamburg (ZMH).

A laboratory stock of N. vitripennis was maintained on Calliphora vomitoria (Linnaeus, 1758) puparia in Petri dishes at room temperature. The stock was originally reared from Protocalliphora azurea (Fallén, 1816) puparia collected from a nest of Parus sp. in Hamburg-Rotherbaum. For laboratory rearing tests on host range parasitoid females were put on puparia or pupae of a variety of Diptera and Lepidoptera species. Parasitoids were taken from the laboratory stock. They were 3–6 days old, mated and fed on moistened raisins. 10 females were put on 30 to 50 puparia or pupae until they died. Hosts included puparia of Triarthria setipennis (Fallén, 1810) (Diptera: Tachinidae) reared from Forficula auricularia Linnaeus, 1758 collected in Hamburg-Rotherbaum, puparia of Protophormia terranovae (Robineau-Desvoidy, 1830), Calliphora vomitoria, Lucilia sericata (Meigen, 1826) (all: Diptera: Calliphoridae; obtained as larvae from bait shops) and Drosophila melanogaster Meigen,

1830 (Diptera: Drosophilidae) and pupae of Galleria mellonella (Linnaeus, 1758) (Lepidoptera: Pyralidae) presented with their cocoons. G. mellonella larvae were reared on artificial medium containing cereals, glycerin, milk powder and honey. All hosts were 4–6 days old. In 2 of the 4 tests with D. melanogaster >100 puparia of different ages from a laboratory mass-rearing were presented.

Additionally, parasitoids were reared on freeze-killed C. vomitoria puparia, which were stored in −28°C 4–6 days after pupation and thawed before a new rearing. All rearings were made in Petri dishes at 24–26°C. If the rearing resulted in a viable F1, it was considered successful, regardless of the number of parasitoid specimens reared. If it did not result in any offspring after four attempts, it was considered unsuccessful.

All data analyses were performed with SPSS 16.0 for Windows. Tests on normal distribution of data were made with Kolmogorov-Smirnov-tests. All significance levels of comparisons were Bonferroni corrected.

RESULTS

Host records.—Nasonia vitripennis was reared from six host species that were collected from birds' nests in the field. These included two species of dipteran bird parasites Protocalliphora spp., the necrophagous Calliphora vicina (all: Diptera: Calliphoridae) and Sarcophaga sp. (Sarcophagidae) and the polyphagous muscid Potamia littoralis. Furthermore, intraordinal hyperparasitism of the dipterophagous braconid Alysia manducator was recorded. In the laboratory, rearing was possible on three additional calliphorid host species and on Triarthria setipennis (Tachinidae). Calliphora vomitoria puparia that were freeze-killed before and then thawed for rearing tests are also suitable hosts for N. vitripennis. Drosophila melanogaster was the only presented Diptera species on which no rearing of N. vitripen-

Table 1.   Host records for *Nasonia vitripennis* from field collections and laboratory rearings; * hyperparasitism in *Calliphora vicina*.

Field host records	Laboratory rearings
Protocalliphora azurea (Fallén, 1816) (Calliphoridae)	**Successful**
Protocalliphora falcozi Séguy, 1928 (Calliphoridae)	*Protophormia terranovae* (Calliphoridae)
Calliphora vicina Robineau-Desvoidy, 1830 (Calliphoridae)	*Calliphora vomitoria* (Calliphoridae)
Potamia littoralis Robineau-Desvoidy, 1830 (Muscidae)	*Lucilia sericata* (Calliphoridae)
Sarcophaga sp. (Sarcophagidae)	*Triarthria setipennis* (Tachinidae)
Alysia manducator (Panzer, 1799) (Hym.: Braconidae) *	*Calliphora vomitoria* (freeze-killed puparia)
	Unsuccessful
	Drosophila melanogaster (Drosophilidae)
	Galleria mellonella (Lepidoptera: Pyralidae)

nis was possible. Also, rearing was unsuccessful on the pupae of the greater wax moth *Galleria mellonella* (Lepidoptera: Pyralidae).

The recorded field hosts of *N. vitripennis* in birds' nests, potential hosts that were confirmed in successful laboratory rearings and examples of species outside the parasitoids' host range are listed in Table 1.

Offspring numbers and sex ratio.—Specimens of *N. vitripennis* emerging from the host species *Calliphora vicina*, *Protocalliphora azurea*, *P. falcozi* and *Potamia littoralis* were counted. In total 5333 individuals from 490 puparia from 17 *Parus* spp. nests were examined (Table 2). All puparia and emerging parasitoids were used for calculation of overall mean of individuals per host and an overall sex ratio (Table 2). 140 puparia were separately stored and were used for comparisons of number of parasitoids per host and proportion of males. These puparia included *Protocalliphora azurea* (N = 16), *P. falcozi* (N = 15), *C. vicina* (N = 72) and *P. littoralis* (N = 37). From these puparia 1897 parasitoids emerged.

Mean comparisons made of the parasitoids of separately stored puparia showed that there are significant interspecific differences in numbers of individuals per puparium. The number was higher in *Protocalliphora azurea* (median 23.0) and *P. falcozi* (median 22.0) than in *C. vicina* (median 10.0) and *P. littoralis* (median 8.0) (U-test, $p < 0.001$). The difference between neither the two *Protocalliphora*-species (U-test, $p > 0.7$) nor between *C. vicina* and *P. littoralis* (U-test, $p > 0.1$) was significant.

For mean comparison of proportion of males, puparia from which only males

Table 2.   The total number, the number per puparium and the proportion of males of *Nasonia vitripennis* in field host species; * = puparia with emergence of only males excluded; ** = recorded from separately stored puparia with reduced sample size.

host species	Calliphora vicina	Calliphora vicina *	Protocalliphora azurea	Protocalliphora falcozi	Potamia littoralis
total no. of host puparia	389	378	47	17	37
total no. of *N. vitripennis*	3614	3530	929	436	354
total no. of ♀	2334	2334	699	379	303
total no. of ♂	1280	1196	230	57	51
overall mean no. per host	9.3	9.3	19.8	25.7	9.6
overall mean ♀	6.0	6.2	14.9	22.3	8.2
overall mean ♂	3.3	3.2	4.9	3.4	1.4
median no. per host **	10.0		23.0	22.0	8.0
maximum no. per host **	28		53	46	25
overall sex ratio ♂:♀	1:1.8	1:1.9	1:3.0	1:6.6	1:5.9
overall proportion of ♂	0.35	0.34	0.25	0.13	0.14
median proportion of ♂ **		0.222	0.155	0.079	0.125

Table 3. Size of puparia of four field host species of *N. vitripennis*.

	Calliphora vicina	*Protocalliphora azurea*	*Protocalliphora falcozi*	*Potamia littoralis*
puparium length (mm)				
median	7.5	7.6	8.4	6.7
interquartile range	2.1	0.8	0.5	0.8
minimum; maximum	4.6; 9.5	6.3; 8.4	7.7; 9.1	6.0; 7.5
length/width				
median	2.34	2.08	2.13	2.78
mean ± std	2.37 ± 0.14	2.1 ± 0.11	2.14 ± 0.08	2.82 ± 0.14

emerged (possibly due to unmated females in the arrhenotokous hymenopterans) were excluded (only in *C. vicina*). The only significant difference after Bonferroni correction is found between *C. vicina* (N = 61) and *P. littoralis* (U-test, p = 0.001). *C. vicina* puparia exhibit a higher proportion of male parasitoids (Table 2). The proportions of males in *P. falcozi* and *P. littoralis* are lower than in *P. azurea*, but these differences are not significant (U-test, p = 0.04, p = 0.047). There is no difference between *P. falcozi* and *P. littoralis* (U-test, p > 0.6). The difference between *C. vicina* and *P. azurea* is also not significant (U-test, p > 0.2). The overall sex ratio measured as the number of females per male was higher in *P. falcozi* and *Potamia littoralis* than in all other species (Table 2; χ^2, p < 0.001). The lowest value compared to all other species was found in the *C. vicina* puparia (p < 0.001). There was no difference if the puparia from which only males emerged, were excluded (p > 0.1).

The host puparia were of different size depending on species (Table 3). The puparia of the *Protocalliphora* species were particularly big, wide and massive. *P. falcozi* puparia are significantly longer than *P. azurea* puparia (U-test, p < 0.001). Puparia size was remarkably variable in *C. vicina*. The smallest and the largest puparia in the study belong to this species. The mean length of *C. vicina* puparia was significantly greater than *P. littoralis* (U-test, p < 0.001), but smaller than *Proto-calliphora* spp., although the length difference with *P. azurea* is not significant (U-

test, p > 0.1). On average the puparia of *P. littoralis* are the smallest. Their shape is rather slim which is shown in the high length to width ratio (Table 3).

DISCUSSION

Host range.—Dominant field host species of *N. vitripennis* from the specific primary habitat (birds' nests) were bird blowflies (*Protocalliphora azurea* and *P. falcozi*), the necrophagous blowfly *Calliphora vicina* and the polyphagous muscid *Potamia littoralis*. The puparia of the parasitic and the necrophagous blowflies appear in the nests when either live or dead nestlings are available. The activity of *N. vitripennis* is linked to the birds' breeding season and largely restricted to the summer months (Schlein 2002). During this time the parasitoid can use the blowfly hosts, the predominantly necrophagous summer generation of *P. littoralis* and, additionally, other necrophagous taxa occurring less frequently like *Sarcophaga* spp. (Table 1). There is no evidence of parasitism of other nidicolous taxa, such as lepidopterans, in this study nor in Noyes (2007).

Successful rearing on the tachinid *Triarthria setipennis*, a parasitoid of earwigs, and on other calliphorid species like *Calliphora vomitoria*, *Lucilia sericata* and *Protophormia terranovae* supports the general use of cyclorrhaphous hosts (Table 1). It demonstrated that *N. vitripennis* can parasitize taxonomically related hosts, with which the species will not have contact under natural conditions. Further examples of suitable cyclorrhaphous hosts of *N. vitri-*

pennis that have been recorded in various studies are *Musca domestica* Linnaeus, 1758, *Muscina stabulans* (Fallén, 1817) and *Stomoxys calcitrans* (Linnaeus, 1758) (all: Muscidae) (e.g. Rivers and Denlinger 1995; Blanchot 1995; Gibson and Floate 2004). Rearing on the pupae of the wax moth *Galleria mellonella* was not possible. All results imply that Lepidoptera are outside the host range of *N. vitripennis*. The very few records of lepidopteran hosts (Noyes 2007) should be seen as misinterpretations or accidental events.

The first limitation of host range within the Cyclorrhapha is host size. Puparia are not parasitized if they are too small, even if they appear in suitable habitats, like the frequent birds' nest species *Tephroclamys tarsalis* (Zetterstedt, 1847) (Heleomyzidae) (Noyes 2007; Peters 2007). It was not possible to rear *N. vitripennis* on *Drosophila melanogaster* in the laboratory, which corroborates the observations of Rivers and Denlinger (1995). A threshold in host suitability regarding puparium size might be represented by the cheese-fly *Piophila casei* (Noyes 2007) (puparia length 4–5 mm). The smallest parasitized puparium in this study was 4.6 mm (Table 3).

A second limiting factor of host range is the shape of puparia: Aberrant forms like the puparia of fanniids, with their conspicuous appendages, are not or not regularly parasitized (only two records: Legner et al. 1967; Blanchot 1995); the almost circular louse fly puparia (Hippoboscidae) are not suitable hosts either (only one record from *Pseudolynchia canariensis* (De Santis 1967)). Like in *N. vitripennis*, host shape as an important host acceptance cue is known from e.g. *Melittobia digitata* (Eulophidae) (Cooperband and Vinson 2000).

A third decisive factor is the host surface structure: *N. vitripennis* hyperparasitizes *Alysia manducator* (Hymenoptera: Braconidae: Alysiinae) inside *Calliphora vicina* puparia as the surface structure indicates a suitable and intact host. The same can be found to explain the parasitism of freeze-killed hosts (Table 1). Although the content of the puparium is completely different from a live pupa in shape and consistency, the host is accepted. An examination of the host pupae with the ovipositor, as described for *N. vitripennis* by Edwards (1954), is therefore unlikely, at least for its impact on host acceptance. The discrimination of hosts using cues of puparia and not cues of their content was recorded for *N. vitripennis* by Smith (1969). In a more general statement Rivers (1996) concluded from his studies that host acceptance in *N. vitripennis* is related to exterior cues of the puparia. These cues are now specified as size, shape and surface structure.

In summary the host range of *Nasonia vitripennis* is defined as:

Polyphagous; Cyclorrhaphous Diptera, especially Calliphoridae, Muscidae and Sarcophagidae at least 4–5 mm in size, excluding puparia with appendages (Fanniidae) and aberrant shapes (Hippoboscidae), including hyperparasitism of Alysiinae in suitable host puparia.

Offspring numbers and sex ratio.—The *Protocalliphora* puparia showed the highest parasitoid numbers while the puparia of *Calliphora vicina* and *Potamia littoralis* had on average significantly fewer (Table 2). Puparia of *Protocalliphora* spp. are larger, which indicates a correlation between host size and number of individuals in the field, although it appears nonlinear: The *C. vicina* puparia are often smaller than the *Protocalliphora* puparia (Table 3), but the size difference is not as big as the difference in parasitoid numbers. Furthermore, *C. vicina* puparia are larger than the *P. littoralis* puparia (Table 3), but the number of parasitoids does not differ. Taken together, *C. vicina* individuals seem to be a less suitable host, independent of host size. The reasons for this are unclear. One possible influential factor is that puparia of *C. vicina* show high variation of puparia size (Table 3), explained by limited food resources (carrion) during the larval development, which results in small specimens and

maybe lower host quality while the parasitic *Protocalliphora* spp. and the small *P. littoralis* have distinctly less variation of puparia size (Table 3).

The correlation between host size and number of parasitoids was also recorded by Wylie (1967) and Rivers and Denlinger (1995) under laboratory conditions. Consequently there is a preference of *N. vitripennis* for larger hosts if choice is possible, recorded by Wylie (1967) and corroborated in field studies, whereas the parasitism rate of the smaller *P. littoralis* increases if the larger calliphorids are missing from a birds' nest (Peters and Abraham 2004).

Field records of parasitoid numbers of *N. vitripennis* in the literature correspond quite well with the average parasitoid number from this study (16.1 parasitoids per host) but are rather rare and restricted to few larger hosts. Gold and Dahlsten (1989) recorded between 15 and 20 parasitoids from *Protocalliphora* spp., Draber-Monko (1995) collected *P. azurea* puparia from tree sparrow nests and recorded a mean number of 20 *N. vitripennis*, but the sample size was small. Marchiori (2005) collected puparia of *Peckia chrysostoma* (Sarcophagidae) and noted a mean number of 15.2 *N. vitripennis* specimens. Molbo and Parker (1996) did not differ between *Protocalliphora* and *Calliphora* hosts and recorded a mean of 26 *N. vitripennis* from both species in the field. The results of Schlein (1998, 2001) using *Calliphora vomitoria* as host species indicate a significant difference between field and laboratory conditions: An average of 33 *N. vitripennis* specimens were reared from *Calliphora vomitoria* in the laboratory (Schlein 2001). In the field numbers were distinctly lower with a mean of 15.7 specimens from the same host species (sentinel puparia placed inside the nest boxes) (Schlein 1998).

The results show that there are interspecific differences between host species and indicate that a correlation of parasitoid numbers and host size is present under natural conditions, but taxonomically restricted exceptions exist. Identifying the factors that underlie the differences in parasitoid numbers per host needs further experiments with different host species and values like parasitoid individual body size, developmental time and mortality rate to be included.

Some differences in proportion of males emerging from puparia were recorded between host species, but no consistent correlation was indicated between sex ratio and host size (Table 2 and 3). Host quality model predictions (larger hosts exhibit more parasitoid females) cannot be found in our field data. The field recorded proportion of males especially in the abundant *C. vicina* and *P. azurea* are higher than expected assuming host-quality control. The sex ratio in the smallest host, *P. littoralis*, is more female-biased than expected. Other factors than host size must be considered for sex ratio determination. Accordant with the predictions for a species that shows local mate competition (LMC), Werren (1984) recorded a higher proportion of males in previously parasitized hosts (superparasitism) for *N. vitripennis*. A further factor affecting sex ratio, which is also related to LMC theory, is the number of ovipositing females in the host patch, with increasing proportion of males if more females are present (Charnov et al. 1981; King and Skinner 1991; Grillenberger et al. 2008). However, Burton-Chellew et al. (2008) showed that offspring sex ratio in natural populations was not directly influenced by number of females in the patch but only by relative clutch size. Besides LMC theory there are other demonstrated influences on sex ratio in *N. vitripennis*: Asymmetric larval competition between sexes is shown to favour less female-biased sex ratios as under larval competition females are smaller when a higher proportion of females was competing within a host (Sykes et al. 2007). Smaller females then produce less offspring (Charnov and Skinner 1984; Sykes et al. 2007). Shuker et

al. (2006) showed that not only females but also males can have an effect on sex ratio, although underlying reasons for this effect are still unclear. The effect might be due to differences in sperm quality between male strains or due to active male influence in order to increase female offspring, i.e. to increase fertilisation and therefore increase contribution to next generation. However, both influencial factors are considered weak when compared to LMC (Shuker et al. 2006; Sykes et al. 2007). Constrained females which can produce only males obviously have effect on sex ratio. In this study hosts from which only males emerged were excluded from comparisons, but in superparasitized hosts we could not control the effect. An indirect effect of constrained females was shown to be absent in *N. vitripennis* by King and D'Souza (2004): The presence of a con-strained female did not influence offspring sex ratios of non-constrained females. Abraham and König (1977) studied the influence of temperature during oviposi-tion on sex ratio in *N. vitripennis*. At lower temperatures less eggs are laid per host with a more female-biased sex ratio. They explain these results with differential mor-tality: less females and more of the smaller males are able to finish development the more larvae are developing within one host.

Recently, Grillenberger et al. (2009) studied the influence of multiparasitism on sex ratio in *N. vitripennis* and the closely related *N. giraulti*. They showed that multi-parasitim in this case has no effect on sex ratio. In our studies we recorded no multiparasitism although multiparasitism with *Pachycrepiodeus vindemmiae* (Rondani, 1875) is known to occur in the Central European study area (Peters 2007). An-other factor that might indeed influence sex ratio is host age which was recorded as influencial for the solitary *Spalangia* sp. (King 2000) and might also have an impact on sex ratio in the gregarious *N. vitripennis*. In this study the only known factor among all these reported influences is host species and size. Number of females, degree of superparasitism, differences between mat-ing males, oviposition temperature etc. are unknown.

Other known data on the sex ratio of *N. vitripennis* show a tendency towards lower proportions of males than in this study (especially when compared to the overall proportion of males, Table 2) but also display a wide range depending on various factors. In Schlein's (2001) laboratory rear-ings of *N. vitripennis* on *C. vomitoria*, the proportion of males was 0.17. In the studies of Abraham and König (1977) on another calliphorid host, *Phormia regina*, the ratio ranges from 0.125 to 0.2 depending on the temperature. Comparable ratios were found by Rivers and Denlinger (1995) for three larger sarcophagid host species in the laboratory. The exception in their studies was a proportion of males of 0.41 within the smaller *Musca domestica*. Two studies on the sex ratio of *N. vitripennis* in natural populations and natural host species re-corded a mean proportion of males of 0.19 in unidentified *Calliphora* sp. and *Protocal-liphora* sp. (Molbo and Parker 1996) or report a wide range dependant on wasp population size (Werren 1983; host species: various necrophagous Cyclorrhapha). The recent studies of Grillenberger et al. (2008) and Burton-Chellew et al. (2008) on natural populations of *N. vitripennis* were done with a mixture of bait hosts and unidenti-fied natural hosts and thus provide no additional information on the role of host species.

As discussed above, factors affecting parasitoid sex ratios are complex and cannot be solved here. However, our results indicate that host species should be considered when studying the influ-ences on proportion of males in host patches and parasitoid populations. This study initially shows data of *N. vitripennis* under field conditions and in identified field hosts which have been very rarely studied before.

ACKNOWLEDGMENTS

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